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DEFENSE STRATEGIES OF FOREST HERBS ON GREAT LAKES' ISLAND AND MAINLAND SITES:
DOES UNGULATE-BROWSE HISTORY PLAY A ROLE?

Introduction. Tolerance and resistance are alternative strategies of plants to defend against herbivory (Strauss and Agrawal 1999). Resistance traits effectively reduce rates of herbivory, through decreased herbivore preference or performance. Tolerance traits allow relatively high fitness despite herbivory. Both forms of defense are potentially costly, and trade-offs will occur between allocation to different defensive strategies, and between defense and other plant functions (e.g. growth and reproduction; Chapin et al. 1990, Lehtila 1999).

One possible tolerance mechanism in plants is storage of reserves. Reserve storage can serve multiple functions, for example, as an adaptation to the asynchrony of resource supply and demand, or as a form of risk aversion (Chapin et al. 1990). By storing reserves, a plant can recover from catastrophic events, such as fire or herbivory. Reserve storage can occur across different time scales, from daily to lifetime storage. Daytime storage supports nighttime respiration, while seasonal storage can promote rapid spring growth in forest understories when light resources are at their maximum. Lifetime storage can allow a transition from a vegetative to reproductive phase.

I propose that seasonal or lifetime reserve storage can also serve as a possible tolerance adaptation of forest herbs to ungulate herbivory, but that there may be a trade-off between resistance and tolerance. I also propose that, in the long-term absence of ungulate herbivory, forest herbs will invest less in long-term storage and resistance.

Study System. We will test these hypotheses through sampling studies and clipping experiments on ungulate-free Great Lakes islands and ungulate-browsed mainland sites. We will target island systems that were historically ungulate free prior to Euro-American settlement. Holocene plant communities that have developed in the absence of ungulate browse pressure should have herb populations that invest more in growth and reproduction and less in defense. Initially, our experiments and sampling will be restricted to Sleeping Bear Dunes National Lakeshore (SLBE), including North and South Manitou Island (NMI and SMI, respectively), and SLBE mainland sites.

We have already begun an investigation of forest herbaceous community recovery from chronic overbrowse by white-tailed deer (*Odocoileus virginianus*) on NMI. Preliminary data suggest that recovery of perennial forest herbs on NMI is happening, but perhaps not in an expected manner. *Trillium grandiflorum*, for example, is recovering quite well despite conventional wisdom that this highly palatable, intolerant forest herb should show greater legacy impacts than either more resistant (e.g. *Arisaema triphyllum*) or tolerant (e.g. *Viola* spp.) species (Augustine and deCalesta 2003). If conditions on SMI represent species potential, then *T. grandiflorum* shows 68% recovery, compared to 12% for *Viola*, and 3% for *A. triphyllum*. Either *T. grandiflorum* is recovering more rapidly, or population impacts of deer were less than for *Viola* and *A. triphyllum*.

Contrary to conventional wisdom, *T. grandiflorum* may be quite tolerant of browse. In assigning forest herb species to relative tolerance levels, Augustine and deCalesta (2003) defined tolerance as capacity for regrowth within a growing season. *T. grandiflorum* and *A. triphyllum* have no capacity for regrowth after browse within a growing season. Therefore, these species were defined as intolerant. I believe that for summer green herbs that emerge in early spring, long-term (between season and lifetime) storage may play an important tolerance function in *T. grandiflorum*, but not in *A. triphyllum*. Previous resource allocation studies have demonstrated a high long-term storage capacity (up to 40% of total plant biomass in storage for > one year) in *Trillium* (Lapoite 1998) but limited capacity for long-term storage in *Arisaema* (Ohara 1989). If this is the case, then *T. grandiflorum*'s tolerance strategy actually appears to have worked quite well on NMI, relative to defense strategies of other forest herbs, such as *A. triphyllum*.

Methodology. We will test the hypothesis that *T. grandiflorum* is more ungulate browse tolerant than *A. triphyllum* through use of clipping experiments. To assess whether species' populations in browse free systems show less resistance and/or tolerance, we will measure chemical defense in *A. triphyllum* (i.e. calcium oxalate crystals) and storage characteristics in *A. triphyllum* and *T. grandiflorum* at both mainland and South Manitou Island sites. All sites will be located in mature beech-maple northern hardwood forest with gentle topography and loamy sand substrates.

Clipping experiments will occur at three mainland and three island sites. At each site, we will locate and permanently tag 30 flowering *T. grandiflorum* plants, and 40 male-flowering *A. triphyllum* plants. We will randomly assign *T. grandiflorum* plants to a control or one of two clipping treatments (early and late season). For *A. triphyllum*, we will add an additional clipping treatment (early, middle, and late season), because its summer green period is longer than *T. grandiflorum*'s. Clipping treatments will occur in late May, early July (just prior to full maturation of *Trillium* fruit), and early September (prior to *A. triphyllum* leaf senescence). Prior to clipping, we will measure leaf height, leaf area and basal stem diameter of each plant. To determine effect of treatment we will record these same measurements for each plant the following year (2007), and treatment effect will be quantified as differences in relative growth rate. We will analyze clipped *A. triphyllum* leaves for calcium oxalate content via a light microscopy method described in Ward et al. (1997).

To assess storage characteristics, we will permanently mark 36 large, nonflowering individuals of each species at both island and mainland site after full leaf expansion in middle to late May, 2006. In 2007, we will harvest 6 marked individuals (3 each at island and mainland sites) of each species every two weeks, beginning with initial emergence and ending with full dormancy in late October, 2007. At each harvest, we will divide the plant into functional units (e.g. roots, rhizomes, stems, or leaves), and then oven-dry and weigh each unit for biomass allocation comparisons. For below ground storage organs (*T. grandiflorum* rhizomes and *A. triphyllum* corms), we will also measure wet volume in order to calculate organ density. Higher relative biomass and lower turnover rates in storage organs should indicate a greater reserve capacity and thus greater tolerance of herbivory.

Relevance to Basic Science and NPS Management .Our research underscores the tight functional relationships between human activity, deer overbrowse, and the direct and indirect effects associated with the imprint of complex and enduring anthropogenic legacies on forest ecosystems. In particular, understanding plant functional traits in relation to historical patterns of browse has implications for assessment of plant community vulnerability to overbrowse, and for restoration of plant communities following chronic overbrowse. Plant communities that have evolved in the absence of ungulate herbivory may be uniquely susceptible to the effects of browse if they are composed of populations that have reduced herbivore defense mechanisms. Such a scenario would provide a compelling argument for restoring or maintaining the ungulate-free status of Great Lake's islands

Schedule. We will initiate clipping experiment in spring and summer of 2006, and finish in spring, 2007. We will measure calcium oxalate levels in *A. triphyllum* leaves during summer 2006, and measure resource allocation and storage characteristics of belowground organs in spring, summer and fall, 2007. We anticipate completing analysis and submitting a manuscript in late fall or winter 2007.

References

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